Revaluation of geometric cues reduces landmark discrimination via within-compound associations

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Abstract

Rats were trained in a triangular water maze in which a compound of geometric and landmark cues indicated the position of a submerged platform. Rats that then underwent revaluation of the geometric cues in the absence of the landmarks subsequently failed to discriminate between the landmarks. In contrast, those animals that received geometry training consistent with their previous experience of the geometry-landmark compound continued to discriminate the landmark cues. The experiment showed that within-compound associations had formed between the geometry and landmarks, and that representations of absent geometric cues could be evoked via presentation of the landmark cues alone. We argue that these evoked representations of the absent geometry cues can counteract any overshadowing of the landmark by geometry cues and may sometimes result in potentiation. The results of this study do not support theories for cue-competition failure based on independent cue processing but remain readily explicable by appeal to an account based on within-compound associations.

KEYWORDS: cue competition, spatial learning, within-compound association, water maze, geometry

Author note

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A recent paper by Austen, Kosaki, and McGregor (2013) demonstrated the presence of within-compound associations between the geometric cues provided by environmental shape and discrete landmarks when both were associated with a goal location. They trained rats to locate a submerged platform with reference to a compound of geometric and landmark cues in a water maze. The platform was located in one corner of a triangular arena, with a landmark cue suspended over it. In the mirror opposite corner, a different landmark was present and together these cues indicated the absence of the platform. Following this training, half of the animals were given landmark revaluation training in the absence of geometric information. On half of the trials the landmark that previously indicated the location of the platform was present but now indicated the absence of the platform. On the remaining trials, the landmark that initially indicated the platform's absence now indicated its presence. A second group of animals was trained similarly, except that the landmark-platform contingencies remained consistent with initial training. In a test trial at the end of revaluation training, rats were placed into the triangular arena in the absence of the landmark cues and the platform, and the time spent searching for the platform with respect to the geometric cues was recorded. Those animals that had undergone revaluation of the landmark cues failed to discriminate between the geometric cues, despite the geometric cues consistently indicating the location of the platform during training. In contrast, those animals that had undergone consistent landmark training continued to discriminate between geometric cues. Austen et al. argued that this revaluation effect was a consequence of the formation of associations between the landmark and geometry cues during initial compound training. Experience of the geometric cues during the test evoked representations of the landmark cues with which they were initially paired. For those animals that had undergone landmark revaluation, such a representation was no longer consistent with the platform's presence and discrimination of the geometric cues was poor (see also Horne & Pearce, 2009; Rhodes, Creighton, Killcross, Good, & Honey, 2009).

The existence of these within-compound associations presents a challenge to the notion that geometry learning progresses independently of learning based on non-geometric cues (Cheng, 1986). They are able to provide an account for apparent failure to observe overshadowing (e.g., Hayward, Good, & Pearce, 2004; Hayward, McGregor, Good, & Pearce, 2003), which has previously been taken as evidence in favour of independent learning of geometric and non-geometric cues (Pearce, Ward-Robinson, Good, Fussell, & Aydin, 2001; Wall, Botly, Black, & Shettleworth, 2004). Within-compound associations can also explain the facilitation of geometry learning following training with a compound of geometric and non-geometric cues, an effect known as potentiation (Cole, Gibson, Pollock, & Yates, 2011; Graham, Good, McGregor, & Pearce, 2006; Horne & Pearce, 2011; Kelly, 2010; Pearce, Graham, Good, Jones, & McGregor, 2006). Austen et al. (2013) discussed the mechanism by which within-compound associations can govern the extent to which cue competition is observed. They acknowledged that when geometric and non-geometric cues are trained concurrently, not only do within-compound associations form between the

geometric and non-geometric cues, but associations also form between the non-geometric cues and the platform, and the geometric cues and the platform. These associations are subject to competition, such that an association between the non-geometric cues and the platform would overshadow a geometry-platform association. The salience of the non-geometric cues determines the extent to which the geometry-platform association is overshadowed. However, the effect of the within-compound association would counteract the overshadowing effect of the non-geometric cue on geometry learning, with the resultant level of cue-competition observed dependent on both the strength of the within-compound association and the strength of the overshadowing effect. To illustrate, a less salient non-geometric cue would only weakly overshadow the geometry, and the within-compound association would more than compensate for its effect, resulting in potentiation being observed. The within-compound association would fail to compensate for the overshadowing effect of a more salient non-geometric cue, such that either overshadowing or a failure of overshadowing would be observed.

Most of the literature has focussed on the effects of non-geometric cues on learning with respect to geometric cues. However, McGregor et al. (2009) examined the reverse effect by training animals in a water maze to locate a platform with respect to both geometric and non-geometric cues and determining the amount learned about the non-geometric cues. Comparison with a control group trained with only non-geometric cues showed that the presence of the geometric cues potentiated learning about the non-geometric cues. In addition, unpublished work from our laboratory, using different cues to those used by McGregor et al. (2009) but that were identical to those used in the current study and by Austen et al. (2013), has shown that geometric cues neither overshadowed nor potentiated learning about non-geometric cues. If these effects are due to the presence of within-compound associations between the geometric and non-geometric cues, as predicted by Austen et al. (2013), then this absence of overshadowing suggests that the effect of the within-compound association is likely to be fairly strong, and so we should be able to demonstrate their presence using a procedure similar to that used by Austen et al.

The design of this experiment was similar to that of Experiment 3 in Austen et al. (2013), with the exceptions that the revaluation stage involved revaluation of the geometry, rather than the landmark cues, and the effect of this revaluation was tested by observing the animals' subsequent discrimination of the landmarks (see Figure 1). Should revaluation of geometry reduce landmark discrimination then this would provide strong evidence for the presence of within-compound associations, which themselves are able to explain the absence of overshadowing in our unpublished experiments, and even potentiation of non-geometric cues by geometry (McGregor et al., 2009).

Method

Subjects. The subjects were twenty male Lister Hooded rats (*Rattus norvegicus*) supplied by Harlan Olac (Bicester, Oxfordshire, England). They were between 200 and 250 g at the start of testing, and had not previously been used in any other study. The animals

were housed in pairs in cages in which they had continuous access to food and water. These cages were in a light-tight holding room on a 12 h light:dark cycle, with lights coming on at 8:00 am. The animals were always tested when the lights were on in their holding room, and at a similar time each day.

Apparatus. A white fiberglass Morris water maze, with a diameter of 2 m and a depth of 60 cm, was mounted on a platform 40 cm above the floor. The water maze was filled to a depth of 30 cm with water (25 ± 2 °C) and white opacifier (500 ml; OP 303B; Rohm & Haas, Dewsbury, England). After each session, the pool was drained and cleaned along with all other apparatus in contact with animals. The pool was fully surrounded by a grey curtain, which prevented the animals being able to utilize any visual extra-maze cues. This curtain formed a circular enclosure of 2.5 m diameter, and extended from the ceiling to 25 cm beneath the top of the water maze. Suspended directly above the pool, at a height of 1 m above the top of the walls, was a white circular polyurethane sheet, 2 m in diameter. This sheet acted as an artificial ceiling and contained eight 45 W spotlights (each 22.5 cm in diameter) arranged in a circular array with a diameter of 1 m. These spotlights illuminated the pool throughout the experiment. A 30 cm diameter circular hole in the center of the spotlight array allowed a wide-angled video camera, which was set 5 cm above the artificial ceiling, to relay an image of the water maze to a monitor, recording equipment, and a PC in the north-east corner of the room. Tracking software (EthoVision, Noldus, NL) was used to record the rats' locations within the pool during the experiment. The pool, curtains and artificial ceiling were situated in the approximate center of a room with dimensions 4.65 x 3.90 x 2.25 m high, with a door situated in the north 3.90 m wall.

Training was conducted within a triangular-shaped arena. To create this arena, two white polyurethane boards, 180 cm in length, 59 cm high and 0.5 cm thick, were attached to lengths of aluminium tubing (1.2 cm square cross-section), which extended 10 cm further than either end of the polyurethane boards in order to suspend the boards within the water maze by resting the aluminium tubing on the top edge of the pool. The third wall of the triangular-shaped arena was formed from the curved wall of the circular water maze. During training, a 10 cm diameter circular Perspex platform was submerged 2 cm below the surface of the water. The surface of this platform consisted of concentric circular grooves to increase traction.

Two landmarks were used in this study. One was a dense sponge ball, 9.5 cm in diameter, painted matte black. The other was a hollow octagonal prism, the inside and outside of which was painted white. The eight walls forming this prism were 9.5 cm tall, 4 cm wide, and 1 cm thick. A 5 mm-thick grey Perspex lid covered the top of the prism. The bottom of the prism remained open, with the exposed edges painted black. Two black stripes were painted horizontally around the center of the prism, each being 2.5 cm wide, with a 1 cm gap separating them. The landmarks were suspended such that the center of each was 30 cm above the surface of the water. This was achieved by attaching each landmark to 8 mm diameter transparent Perspex rods, which were attached horizontally to the aluminium tubing suspending the polyurethane walls. The landmarks were placed at a

distance of 25 cm from the corners of the triangular arena that were made up from one straight wall and the curved base, on a line bisecting each corner.

The pre- and post-revaluation landmark tests used the entire circular water maze as the arena. Within this, the two landmarks were suspended by thin white wires from the artificial ceiling, such that the distance between the center of each landmark and the surface of the pool was 30 cm. The landmarks were situated along an imaginary line that bisected the circular arena in a north-east to south-west direction. Each landmark was suspended at a distance of 63 cm from the wall of the water maze.

Procedure. Training for all animals consisted of 18 sessions of four trials per session, with one session per day. At the beginning of each session, rats were transported to the testing room in separate compartments of a light-tight carrying box. This box was placed onto a table in the north-west corner of the room. During training a rat was removed from the carrying box and placed into the water maze at the center of one of the three walls, facing the wall. The rat swam until it found the platform, after which it was allowed to remain on the platform for 20 s before being removed from the pool, dried, and returned to the carrying box for an inter-trial interval of approximately 5 minutes. If an animal failed to locate the platform within 60 s, it was guided there by the experimenter, where it remained for 20 s before being removed and dried in the usual manner. Throughout the experiment, the curtains were drawn around the pool such that the animals were unable to use any visual cues beyond the curtain to locate the platform. Release points were counterbalanced such that for the four trials of a session, each release point (one from each wall, three in total) was used once, with the final release point being chosen randomly, with the stipulation that across three sessions each release point was used an equal number of times. The orientation of the arena was varied between trials, with each of the four possibilities (i.e., the apex of the arena pointing towards each cardinal compass point) used in each session, in a pseudorandom order. The identity of the correct landmark was counterbalanced, such that five animals in each group experienced the platform underneath the ball landmark, with the platform being located underneath the prism landmark for the remaining animals. For both groups, the corner in which the platform was located was counterbalanced, such that six animals were trained to find the platform in one of the base corners of the triangle, with the straight wall to the left of the curved wall, with the other four animals finding the platform in the other base corner, which had the opposite arrangement of walls.

All animals then received a pre-revaluation landmark test to determine the extent to which landmark cues had gained control of their behavior. This test proceeded in the absence of the platform. The locations of the landmarks within the pool were fully counterbalanced, such that half of the animals received the prism, and the other half the ball, in the north-east quadrant of the pool. For half of the animals, the correct landmark was located in the north-east quadrant, with the remainder finding it in the south-west quadrant. Animals were released from the center of the pool, equidistant from the two landmarks, and allowed to search for the absent platform for 60 s.

This pre-revaluation landmark test was then followed by a revaluation stage. This was the first stage in which the training experienced by the two groups differed. Animals were divided into similar groups, such that both groups were matched on performance during training and the pre-revaluation landmark test. One group would experience consistent landmark-reward contingencies (group CON), while for the other group those contingencies would be inconsistent (group INCON). Groups CON and INCON received eight sessions of training, with four trials per session, in the absence of landmark cues, but in the familiar triangular-shaped arena. Group CON could find the escape platform in the same corner in which it was located during initial training. For group INCON, the location of the escape platform was moved to the previously incorrect corner of the triangular arena. Following the same protocol as during initial training, animals were released from each of the three walls of the arena and the arena was rotated between trials. The corner of the arena first visited after release into the pool was recorded as the measure of revaluation training. An animal was said to have made its *first choice* when its snout had entered one of two zones, created by notional arcs with radii of 40 cm and their centers at the points where the walls creating each corner met.

After this revaluation training, both groups received the post-revaluation landmark test, conducted in exactly the same manner as the pre-revaluation landmark test. A schematic of the procedure used in this experiment can be seen in Figure 1.

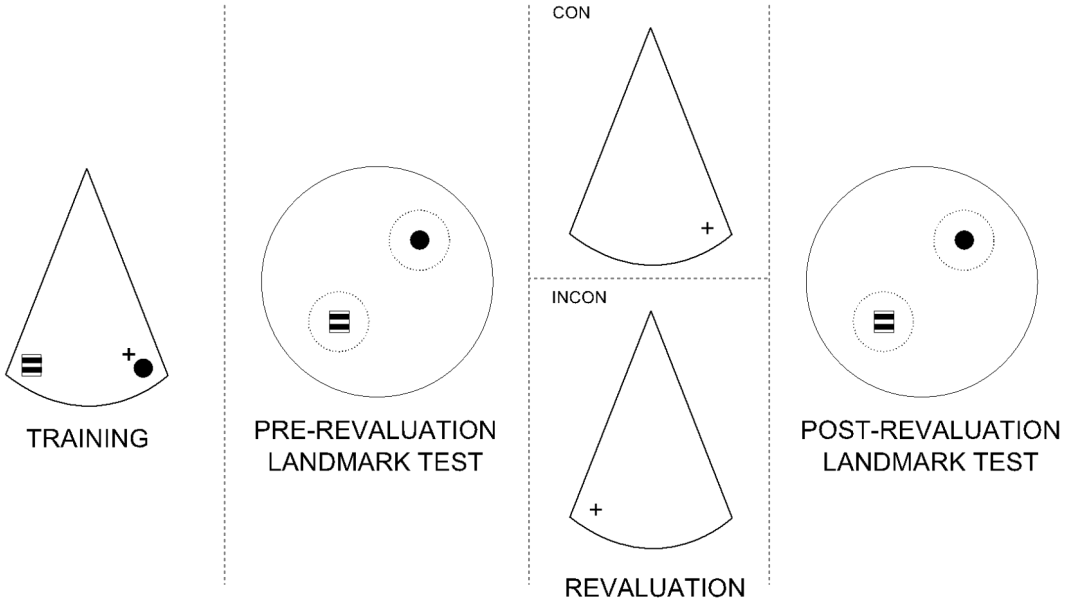

Figure 1*:* Schematic of the experimental design. Plus (+) signs represent the position of the hidden escape platform. Dotted areas denote those places in which exploration times were queried to determine the extent of landmark learning. Although the figure shows only the ball landmark to be rewarded during training, half of the animals received the platform underneath the ball landmark, and the other half underneath the prism landmark.

Results

Training. The latencies (*SEM*) for groups CON and INCON to find the escape platform during training decreased over sessions. Groups CON and INCON decreased from means of 36.9 s (*1.8*) and 29.9 s (*2.5*), respectively, on session 1 to means of 5.3 s (*0.3*) and 5.0 s (*0.3*) on session 18. As all animals were trained identically during this stage, it is no surprise that both groups took a similar amount of time to find the platform. A mixed ANOVA (Group x Session) of mean individual times to locate the platform on each session was conducted. The relevant statistics have been adjusted using the Greenhouse-Geisser correction to account for a lack of sphericity in the session variable. This ANOVA indicated a significant main effect of session, $F(4.4, 79) = 99.5$, $p < .001$, with the time taken to find the escape platform generally decreasing over sessions. This decrease in latencies was similar for both groups, with no significant main effect of group, $F < 1$, and no interaction between session and group, $F(4.4, 79) = 1.99$, $p = .10$.

Pre-revaluation landmark test. Groups CON and INCON spent a similar amount of time (*SEM*) searching beneath both the landmark that indicated the location of the platform during compound training (CON = 7.2 s (*1.3*), INCON = 7.7 s (*2.0*)) and the incorrect landmark (CON = 1.8 s (*0.6*), INCON = 1.3 s (*0.5*)). A mixed ANOVA (Zone x Group) of time spent in the proximity of the landmarks showed a significant main effect of zone, $F(1, 18) = 26.2$, $p < .001$, with more time being spent exploring underneath the correct landmark than the incorrect landmark. There was no significant main effect of group, $F < 1$ and no interaction between zone and group, $F < 1$. It can be inferred from these data that

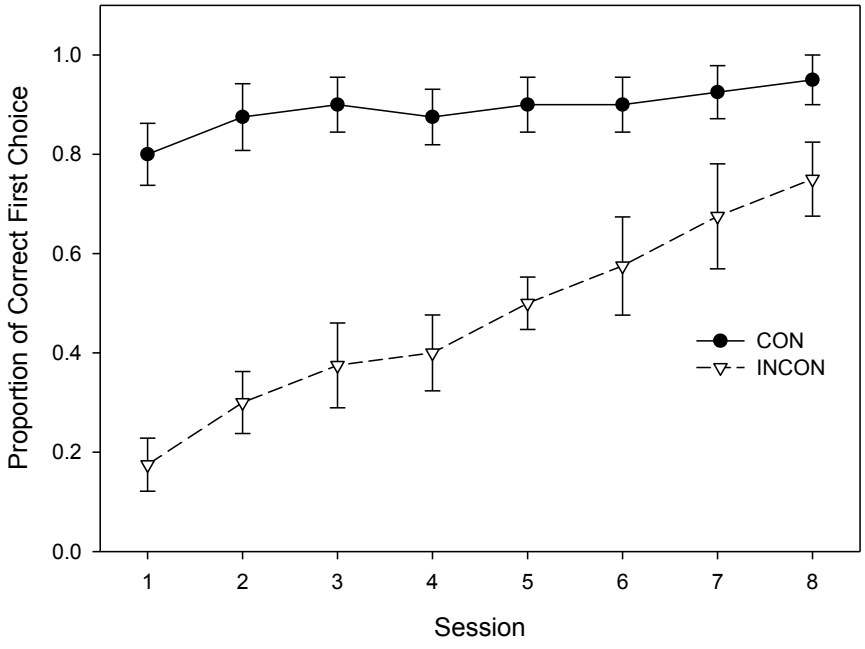

Figure 2: Proportion of correct first choice for groups CON and INCON during the revaluation stage. Error bars represent ± Standard Error of the Mean.

both groups learned a similar amount about the relationship between the correct landmark and the location of the platform. These results are of no surprise given that all animals were trained identically before the pre-revaluation landmark test.

Revaluation. The first choices for groups CON and INCON are shown in Figure 2. Group CON consistently showed a high proportion of first choices to the correct corner across sessions, whereas group INCON began the revaluation stage with a much lower proportion of correct first choices than group CON, but gradually improved over time as they learned the new location of the platform. A mixed ANOVA (Session x Group) of proportion of correct first choices was conducted. The relevant statistics have been adjusted using the Greenhouse-Geisser correction to account for a lack of sphericity in the session variable. There was a significant interaction between group and session, $F(4.2, 75.8) = 3.23$, $p = .015$. Analysis of this interaction showed that for group CON there was no difference in the proportion of correct first choices between sessions, $F < 1$, but this was not the case for group INCON, $F(7, 12) = 11.8$, $p < .001$. Importantly, group INCON made significantly more correct first choices on session 8 than on session 1, $p < .001$. This indicates that group INCON reversed their learning about the position of the platform, as a consequence of the revaluation training.

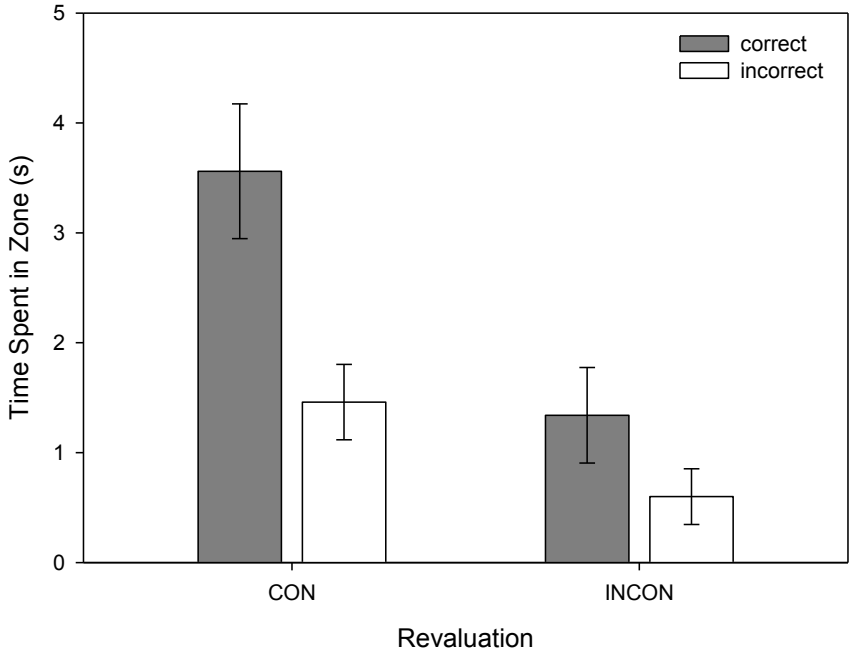

Figure 3: Time spent searching for the hidden escape platform underneath the correct and incorrect landmark cues during the post-revaluation landmark test. Error bars represent ± Standard Error of the Mean.

Post-revaluation landmark test. The result of greatest interest is the post-revaluation discrimination between landmark cues. Figure 3 suggests that while group CON persisted in its ability to discriminate between the correct and incorrect landmark cues,

group INCON searched for the platform similarly underneath each of the landmarks. A mixed ANOVA (Zone x Group) of time spent searching for the platform showed a significant interaction between zone and group, $F(1, 18) = 5.28$, $p = .034$. Analysis of this interaction showed that animals in group CON retained their ability to discriminate between correct and incorrect landmarks, spending significantly more time searching in the correct, rather than incorrect, zone, $F(1, 18) = 25.2$, $p < .001$. Group INCON failed to discriminate between the two landmarks, $F(1, 18) = 3.13$, $p = .094$. Further, Group CON spent significantly more time searching in the correct zone than group INCON, $F(1, 18) = 8.73$, $p = .008$, whereas there was no significant difference in time spent in the incorrect zone between groups, $F(1, 18) = 4.08$, $p = .059$.

Discussion

The data suggest that by revaluing the geometry cues for group INCON, the landmark cues were also revalued, such that animals failed to discriminate between the landmark under which the platform was always located during compound training, and the landmark under which the platform was never located. This failure to discriminate contrasts with the behavior of group CON, which retained its ability to discriminate between the correct and incorrect landmarks. These results can be interpreted in a similar fashion to the interpretation offered by Austen et al. (2013). During the post-revaluation landmark test, group INCON's experience of the initially correct landmark evoked a representation of the geometric cue with which it was paired during training. This geometric cue had been demonstrated to no longer indicate the location of the platform during revaluation, and hence the evoked representation prevented animals from searching underneath this landmark. For group CON, however, this evoked representation would have been a geometric cue that was associated with the platform, and as such group CON retained their discrimination of the two landmark cues.

Whilst it might be argued that the presence of within-compound associations should cause group INCON to show increased interest in the "incorrect" landmark during the post-revaluation landmark test, it can be readily understood why this is not the case. During compound training the animals experienced the correct landmark-corner compound much more frequently than the incorrect landmark-corner compound. It follows, therefore, that the strength of the within-compound association between the incorrect landmark and the incorrect corner was not as strong as between the correct cues. The revaluation of the initially incorrect corner may therefore not have had much of an effect on its associated landmark due to the relative weakness of the within-compound associations between these cues. However, the reduced absolute level of searching in the correct area of the post-revaluation landmark test, when compared with the pre-revaluation landmark test, deserves some comment. Responding to the correct landmark can be seen as the result of two associations: a direct landmark-platform association and an indirect landmark-corner-platform association. In the pre-revaluation landmark test, the landmark-platform association is likely to dominate, as the animals had just completed compound training in

which the landmark and platform were directly paired. By contrast, in the post-revaluation landmark test, the last time that the landmark and platform were directly paired was ten sessions previously. As such, it would be expected that the direct landmark-platform association would have weakened, seemingly reducing responding by more than the strengthened landmark-corner-platform within-compound association could compensate. Indeed, we might also expect that the within-compound associations had been weakened by the revaluation training. The presentation of a single element of a previously rewarded compound, even when that element is rewarded, has been shown to reduce the strength of the within-compound association of that compound (e.g., Rescorla & Freberg, 1978). This weakening would also contribute to the reduced responding towards the landmark cues during the post-revaluation landmark test.

These results not only provide another demonstration that within-compound associations form between landmark and geometry cues trained in compound, but also show that experience of a landmark cue can evoke a representation of the geometry cue with which it was paired during training. Combined with the results of Austen et al. (2013), this demonstrates that within-compound associations can be the mechanism by which either landmark or geometry cues are able to counteract overshadowing of, or potentiate learning about, the other cue type, when trained in compound.

Whilst it has been argued that the evoked representations of absent cues that within-compound associations afford upon experience of a cue that is present explains the reason for the failure to observe overshadowing, other explanations have been put forward, which do not require the presence of within-compound associations. There has been proposed a module dedicated to processing information about geometric features of the environment (Cheng, 1986; Gallistel, 1990). One feature of this module is its impenetrability to non-geometric information. It would therefore be of no surprise that landmark cues are not overshadowed by geometry, as learning about these two types of cue would be predicted to occur separately. However, this explanation would not allow the formation of within-compound associations between the landmark and geometry cues that resulted in the revaluation effects demonstrated in the current article (and, indeed, in Austen et al., 2013). This geometric module would also allow neither the potentiation seen in Austen et al., nor the accounts of discrete landmarks competing with geometric cues demonstrated elsewhere (e.g., Kosaki, Austen, & McGregor, 2013). This same argument can be applied to other accounts of spatial learning that suppose learning based on one cue-type or frame of reference to be independent of another (e.g., Doeller & Burgess, 2008; Wang & Spelke, 2002, 2003). Austen et al. have previously also argued that both template-matching (Cheung, Stürzl, Zeil, & Cheng, 2008; Stürzl, Cheung, Cheng, & Zeil, 2008) and framework stability (Timberlake, Sinning, & Leffel, 2007) fail to account for the kinds of revaluation effects observed in the current paper. It may be argued that the revaluation effect observed in this study is not due to the formation of within-compound associations between the landmark and geometry cues, but instead is a consequence of the revaluation training for group INCON resulting in interference between the newly correct geometric location and

the previously correct landmark cue. Although this is a theoretically possible explanation of our results, accepting this would provide no mechanism for the potentiation effects seen in Austen et al. and elsewhere, or the apparent failure to observe overshadowing between geometric and non-geometric cues described previously.

As within-compound associations seem capable of explaining many seemingly anomalous results from the spatial learning literature, this phenomenon clearly warrants further study. It has yet to be determined exactly under which circumstances these within-compound associations arise in spatial learning, and whether, for example, the relative saliences of the cues affects the strength of the association between them. Bouton, Dunlap, and Swartzentruber (1987) showed that taste-taste compound training led to potentiation of one of the tastes only when it was weakly conditionable when presented on its own. They proposed that such a situation promoted the perceptual integration of the flavors such that the potentiated cue was perceived as a feature of the other flavor (for similar effects in taste-odor learning see also Bouton, Jones, McPhillips, & Swartzentruber, 1986). Manipulation of the relative saliences of the non-geometric and geometric cues used in our studies would enable us to determine the common aspects of potentiation in different modalities. In addition, there are a wealth of spatial cues between which similar associations may form and act to mediate the level of cue competition observed. Further insight into the presence and consequence of these within-compound associations would allow this evidently crucial, but until now overlooked, aspect of spatial learning to be better understood.

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